

EFFECTS OF FOREST ROADS ON THE ABUNDANCE AND ACTIVITY OF TERRESTRIAL SALAMANDERS

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Abstract. One of the major effects of deforestation is the creation of numerous edge zones where remaining forest meets nonforest habitat. At this interface, edge effects on forest habitats can include altered abiotic conditions, changes in rates of competition and predation, and altered community structure. While the edge effects resulting from clear-cuts and other open habitats are well-studied, little is known about the comparative edge effects of forest roads. We studied the effects of forest roads on the abundance, surface activity, and body condition of red-backed salamanders (*Plethodon cinereus*) and slimy salamanders (*P. glutinosus* and *P. cylindraceus*) in the Southern Appalachians of Virginia. We conducted surveys for salamanders at 21 sites where gravel roads bisected mature forest. These sites were divided into three data sets based on region and year of survey. We also carried out an enclosure experiment to determine whether road edges influenced the surface activity and detectability of red-backed salamanders. We found fewer red-backed salamanders near roads in all three data sets. These edge effects extended <20 m into the forest in two of the three data sets but increased linearly out to 80 m in the data set collected during an unusually dry period. In contrast, slimy salamanders showed no clear responses to forest–road edges and had significantly different responses than those of red-backed salamanders. Within our experimental enclosures, red-backed salamander detectability did not differ between edge and interior habitats, suggesting that the patterns we observed were not simply due to changes in salamander activity patterns. Like red-backed salamander counts, soil moisture and cover object area also tended to decrease near roads. The steepness of the gradient in soil moisture was a significant predictor of the steepness of the decline in salamander counts, while there was no significant relationship between the decreases in cover object area and decreases in salamander counts. Collectively, these results show that edge effects from forest roads may be comparable to edge effects from clear-cuts or other types of silvicultural edges. Additionally, they suggest that, for terrestrial salamanders, variation in the magnitude of edge effects may be related to variation in soil moisture. Management approaches that minimize soil desiccation associated with road building and maintenance may reduce the impacts of roads on amphibian populations in adjacent forest.

Key words: *amphibians; desiccation; edge effects; fragmentation; Plethodon cinereus; Plethodon glutinosus; roads; salamanders; Southern Appalachians (USA).*

INTRODUCTION

Habitat loss is perhaps the major threat to forest-dwelling species (Reid and Miller 1989, Heywood 1995, Fahrig 2002). In addition to the direct effects of habitat loss, deforestation also increases the proximity of forest habitats to nonforest areas such as clear-cuts, agricultural fields, and residential areas. For many species, forest habitat near edges may not be as suitable as interior forest (see Murcia 1995, Harrison and Bruna 1999 for reviews). The collective abiotic and biotic effects of proximity to edges on forest habitats are usually classified as edge effects. Abiotic components of edge effects for forest habitats often include decreased soil moisture and humidity, increased soil temperatures, and increased penetration of light and wind (Chen et al. 1995, Turton and Freiburger 1997, Gehl-

hausen et al. 2000). These abiotic effects can lead to changes in species abundance and community structure. They can also influence biotic interactions by altering rates of predation or parasitism (Brittingham and Temple 1983, Hartley and Hunter 1998). Both abiotic and biotic components of edge effects can extend up to several hundred meters into forest habitats, affecting a large proportion of landscapes in highly fragmented areas (Franklin and Forman 1987, Chen et al. 1995).

Although the concept of edge effects is straightforward, empirical studies of edge effects have produced a more complex picture. First, the distance over which edge effects occur is highly variable among related species (Euskirchen et al. 2001, Flaspohler et al. 2001, Schlaepfer and Gavin 2001). Second, the magnitude of edge effects for individual species may vary depending on season, aspect, and topography (Chen et al. 1995, Cadenasso et al. 1997, Gehlhausen et al. 2000). Edge effects may also depend on the structure of the transition between forest and adjacent disturbed areas,

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PLATE 1. A forest road survey site. Photo credit: D. Marsh.

sometimes referred to as the “edge contrast” (deMaynadier and Hunter 1998, Gehlhausen et al. 2000).

Most previous studies of edge effects have focused on forest–clear-cut or forest–field edges. However, road building in forest areas also creates numerous edge zones, and forest–road edges may differ from forest–clear-cut or forest–field edges in substantive ways. Forest roads are relatively narrow, and may cause only incomplete breaks in forest canopies (Ortega and Capen 2002). Thus, one might expect many abiotic effects of forest–road edges (e.g., increased light and wind penetration) to be less severe than those of other types of edges. Consistent with this, the effects of road edges on understory plants in Wisconsin occur only over relatively short distances (Watkins et al. 2003). On the other hand, roads may have impacts on animals that clear-cuts do not, such as effects of traffic noise, dust and pollution, and direct mortality from collisions with vehicles (see Forman and Alexander 1998 for review). Additionally, road edges are generally more permanent than clear-cut edges, so forest regrowth is unlikely to ameliorate their effects (deMaynadier and Hunter 2000). Forest roads have been shown to decrease the

abundance of leaf litter invertebrates (Haskell 2000) and several species of birds (Ortega and Capen 2002).

Mileage of forest roads in the United States has almost doubled since 1970, though many roads have been decommissioned and shifted to lower levels of maintenance with reduced traffic (USDA Forest Service 1998). Expansion of forest road networks has led to the protection of roadless areas within National Forests (USDA Forest Service 2000), and these roadless areas have been the source of continuing political controversy. Given this controversy, understanding the effects of roads on adjacent forest habitats should be a priority. We focus on the effects of forest roads on populations of terrestrial salamanders in the Southern Appalachian Mountains of Virginia. Terrestrial amphibians are well-suited for studies of edge effects (Schlaepfer and Gavin 2001, Toral et al. 2002) because they have limited mobility and are dependent on soil moisture (Sugalski and Claussen 1997, Grover 1998) and other components of forest habitat quality (Welsh and Droege 2001). In addition, the relationship between terrestrial salamander density and distance from forest–clear-cut edges has previously been quantified (deMaynadier and Hunter

1998, deGraaf and Yamasaki 2002), so responses to forest–road edges can be compared to forest–clear-cut edges.

We used transect surveys to estimate the abundance of terrestrial salamanders at 21 forest sites along gravel roads in two regions (see Plate 1). We asked whether salamander abundance increased with distance from road and compared responses to roads across species, across regions, and across years. We also measured soil moisture and temperature, the abundance of coarse woody debris, and leaf litter thickness and used these data to examine relationships between abiotic factors, distance from roads, and the abundance of terrestrial salamanders. Finally, we used an enclosure experiment to determine whether salamander activity patterns and detectability on the forest floor differ between edge zones and more interior areas.

METHODS

Study species and sites

Red-backed salamanders (*Plethodon cinereus*) and slimy salamanders (*P. glutinosus* and *P. cylindraceus*) were the two most common species within our study regions. Red-backed salamanders are small, terrestrial salamanders found at high densities across much of the eastern United States and Canada. They are usually found underneath logs and rocks on the forest floor, though they emerge on rainy nights to forage in the leaf litter and on low vegetation. A substantial proportion of the red-backed salamander population is usually underground, even during periods of high surface activity (Taub 1961). Thus, surface counts reflect only a subset of the population, though surface counts are highly correlated with mark–recapture estimates of population size (Smith and Petranka 2000).

Slimy salamanders are a complex of 13 species formerly considered to be *Plethodon glutinosus* (Highton et al. 1989). Slimy salamanders within the Mountain Lake region are still designated *P. glutinosus*, while slimy salamanders within the Big Levels region are designated *P. cylindraceus*. We refer to both species as slimy salamanders, though we do not combine data for these two species in our analyses. Slimy salamanders have a similar life history to red-backed salamanders, but are generally larger, less abundant, and more resistant to desiccation (Grover 2000).

We conducted salamander surveys over two years at 21 sites in two regions. These sites were located along 15 roads, with no more than two sites per road. When two sites were used along the same road, these sites were located at least 1 km apart and on opposite sides of the road to increase the statistical independence of sites. With respect to salamander counts, sites along the same road were not statistically more similar than sites on other roads within the same region ($F_{5,5} = 0.39$, $P = 0.84$). Thus we consider each of the 21 sites as an independent replicate.

The “Mountain Lake” region contained a set of 12 sites at 740–1220 m elevation in the Allegheny Mountains of Giles and Montgomery County, Virginia. Salamanders in this region reach very high densities (>2 individuals/m² for red-backed salamanders, Mathis 1991) and are active throughout the relatively cool summers. We selected 12 sites within this region in 2001 by first identifying suitable areas. Our criteria for suitability were: (1) a gravel road bisecting mature forest; (2) no obvious signs of logging or fire; (3) no streams or ponds within 200 m; and (4) slope of the terrain $<30^\circ$. Sites on ridgetops were also excluded. From 11 July to 7 October 2001, we conducted six surveys in the Mountain Lake region. From 22 June to 26 September 2002, we surveyed the remaining six sites. This latter survey period contained an extreme drought in which stream flows hit record lows for many areas of Virginia (Virginia State Climatology Office 2002).

The second region (“Big Levels”) contained nine sites at the base of the Blue Ridge Mountains in Central Virginia. Sites were centered around the Big Levels Management Area and were between 450 and 550 m in elevation. Forest areas in the Big Levels region are generally younger and more disturbed by fire, cutting, and selective logging than forests in the Mountain Lake region. Terrestrial salamander diversity is similar to that in the Mountain Lake region, though densities are lower, temperatures are higher, and terrestrial salamander surface activity is generally restricted to spring and fall. From 27 April to 2 June 2002, we surveyed nine sites within this region.

Transect surveys

We established four, 50-m transects at each site. Transects were located 5, 20, 40, and 80 m from forest edges and ran parallel to the road. Forest edges were generally clearly delineated and were between 2 and 5 m from roads. We selected transect distances based on previous studies showing that edge effects for red-backed salamanders at forest–clear-cut edges extended ~25–35 m into the forest (deMaynadier and Hunter 1998). Starting points for transects were selected from within each suitable area by choosing a random number to use as distance from the border of each suitable area. We surveyed the four transects in a random order. To eliminate bias due to observer effects, the senior author conducted all the searches at the 12 Mountain Lake sites. At the nine Big Levels sites, nine observers were trained and randomly assigned transects such that each observer searched exactly one transect at each distance. Differences among observers did not explain significant variation in salamander counts ($F_{8,16} = 0.80$, $P = 0.61$), so we did not include this factor in later analyses.

Transect searches were conducted by turning over all cover objects (rocks, logs, bark, and other objects) within 2 m of the center of the transect. Leaf litter was not searched. We measured the length and width of

each cover object and recorded the number and species of every salamander found. For red-backed salamanders, we measured snout-vent length and tail length with calipers, and we measured mass using a Pesola 10-g scale (Pesola AG, Baar, Switzerland). We also collected data on habitat variables. We took soil samples by scooping soil into a 33-mL film canister at four randomly selected points along each transect. From these samples, we measured soil moisture by weighing canisters, drying them at 75°C for 48 h, and then reweighing them. We used $(\text{wet mass} - \text{canister mass} - \text{dry mass}) / (\text{wet mass} - \text{canister mass})$ as an index of soil moisture. At the same locations on each transect, we also measured soil temperature using a Reotemp soil thermometer (Reotemp Instrument, San Diego, California, USA), and leaf litter thickness by placing a 20-cm ruler perpendicular to the ground. To avoid variability in habitat measurements due to rainfall, all habitat data were collected on days in which no rain had fallen for three previous days.

Statistical analysis

We initially divided sites into three data sets: Mountain Lake, 2001 (six sites), Mountain Lake, 2002 (six sites), and Big Levels, 2002 (nine sites). We then examined differences among years by comparing the Mountain Lake 2001 data to the Mountain Lake 2002 data. We examined differences among regions by comparing the Mountain Lake data to the Big Levels data.

For red-backed salamanders and slimy salamanders, we calculated the total number of salamanders seen per transect. These counts tended to follow a Poisson distribution, so we square-root transformed them for normality (Sokal and Rohlf 1995) prior to all analyses. We used site as a blocking factor, and analyzed the effects of distance from road edge on transformed counts using General Linear Models (Neter et al. 1996). For significant effects of distance, we conducted post hoc analysis using Scheffé tests on means and by using linear regression to ask whether salamander counts increased or decreased with distance from the road edge. Because only cover objects were surveyed, counts could have been biased if the number or size of cover objects, and thus sampling effort, changed with distance from road. To test this, we repeated the previous analysis with salamanders per cover object and salamanders per cover object area as the response variable.

We also analyzed the effects of distance from road edge on red-backed salamander size and body condition. As an index of size, we used the mean snout-vent length (SVL) for salamanders on each transect. To get an index of body condition we regressed $\ln(\text{mass})$ on SVL and tail length, and took the residuals of this regression as an index of body condition (Harris and Ludwig 2004). We then used a GLM blocked by site to ask whether body size or condition depended on distance from road.

For habitat variables, we calculated the total number of cover objects per transect, the total area of cover objects per transect, the mean soil moisture per transect, the mean soil temperature per transect, and the mean leaf litter thickness per transect. We then used GLMs to ask whether each habitat variable changed with distance from road. We used an alpha of 0.05 for each of these analyses, as this was essentially an exploratory analysis to identify habitat factors that might be related to distance from road edges and salamander counts.

To compare results between species, we added species as an additional factor in a GLM that included distance and site as above. We used the significance of the species \times distance interaction to indicate edge effects that differed between species. We used only the Mountain Lake data for this analysis (12 sites) because slimy salamanders were absent from a number of the Big Levels sites. To compare results across years, we added year to the GLM including site and distance and used the year \times distance interaction as a measure of differences in edge effects across years. To compare across regions, we pooled the Mountain Lake sites, included main effects of region, site, and distance in the GLM, and used the region \times distance interaction as a measure of the differences in edge effects among regions.

For several variables that were correlated distance from road edges, we asked whether the steepness of the gradient in each habitat variable predicted the steepness of the decline in salamander counts near roads. For each site, we calculated the slope of the regression of each habitat variable on distance from road. We also calculated the slope of the regression of salamander count on distance. We then used linear regression to ask whether the slope of the habitat gradient predicted the slope of the gradient in salamander counts. We carried out this analysis at the 12 Mountain Lake sites only because counts for red-backed salamanders at some of the Big Levels sites were too low to produce reliable regression slopes.

Detectability experiment

Red-backed salamanders spend the majority of their time underground. In some surveys, surface counts have been estimated to represent <10% of the overall population, even during times that are conducive to surface activity (Welsh and Droege 2001). If salamanders spend more time underground in harsher environments, lower counts near roads could reflect changes in activity patterns rather than actual changes in population size. To test for this potential bias, we carried out an enclosure experiment near Mountain Lake from July to September, 2001.

We placed two red-backed salamanders marked with fluorescent elastomer tags (Davis and Ovaska 2001) in each of 24 paired enclosures at 12 sites. At each site, one enclosure was located 5 m from the forest edge

(“edge enclosures”) and one enclosure was located 40 m from the forest edge (“interior enclosures”). We selected suitable locations for enclosures using the same criteria we used to establish transect locations, and four of the enclosure sites were within transect locations. Enclosures were 0.9×0.9 m squares with sides 10 cm high and 2 cm wide. Strips of aluminum flashing 12–15 cm wide were attached to the tops of the enclosure to form a lip that prevented salamanders from escaping or entering. The bottom of the enclosure was a deep bag of fiberglass mesh stapled to the bottom of the wood square and sealed with caulk. We established each enclosure by digging out the soil to a depth of ~30–40 cm, placing the mesh bag in the hole, and replacing the soil. We placed two split logs in each enclosure, and we added leaf litter by removing the total amount of leaf litter in the square meter immediately adjacent to the enclosure. Thus, enclosures provided the normal range of habitats available to salamanders, including leaf litter, cover objects, and underground retreats up to 30–40 cm deep.

From 19 July to 24 August 2001, we monitored surface activity of red-backed salamanders. On 19 dates, we censused all cover objects and recorded the location of each salamander. On 10 other dates, we conducted nighttime surveys in which we visually searched the surface of each enclosure with a flashlight for 3 min. At the conclusion of the experiment, we calculated the mean detection rate for each enclosure for both daytime cover object surveys and nighttime surveys. We analyzed the effects of enclosure type (edge vs. interior) on each of these detection rates using two-way ANOVA with site as a block effect. All analyses were performed using SAS version 8.2 (SAS 2001).

RESULTS

Mountain Lake, summer 2001

In 2001, a mean of 10.9 red-backed salamanders and 1.2 slimy salamanders were recorded from each transect. There was a significant effect of distance from road edge on counts of red-backed salamanders ($F_{3,15} = 8.93$, $P = 0.001$, Fig. 1A). In pairwise comparisons, red-backed salamanders were significantly less abundant at 5 m compared to 20, 40, and 80 m, though no other pairwise comparisons approached significance. A linear regression of counts on distance was also non-significant ($b_1 = 0.314$, $t = 1.554$, $P = 0.14$) suggesting that there was no clear tendency for salamander abundance to increase with distance beyond 20 m into the forest. Patterns were quite similar when the number of cover objects and the area of cover objects were taken into account (Fig. 1B, C). For salamanders per cover object, there was an overall effect of distance from the road edge ($F_{3,15} = 4.48$, $P = 0.019$), with significantly fewer salamanders at 5 m compared to 20, 40, and 80 m. For salamanders per square centimeter of cover object, results were nearly identical, with an overall effect

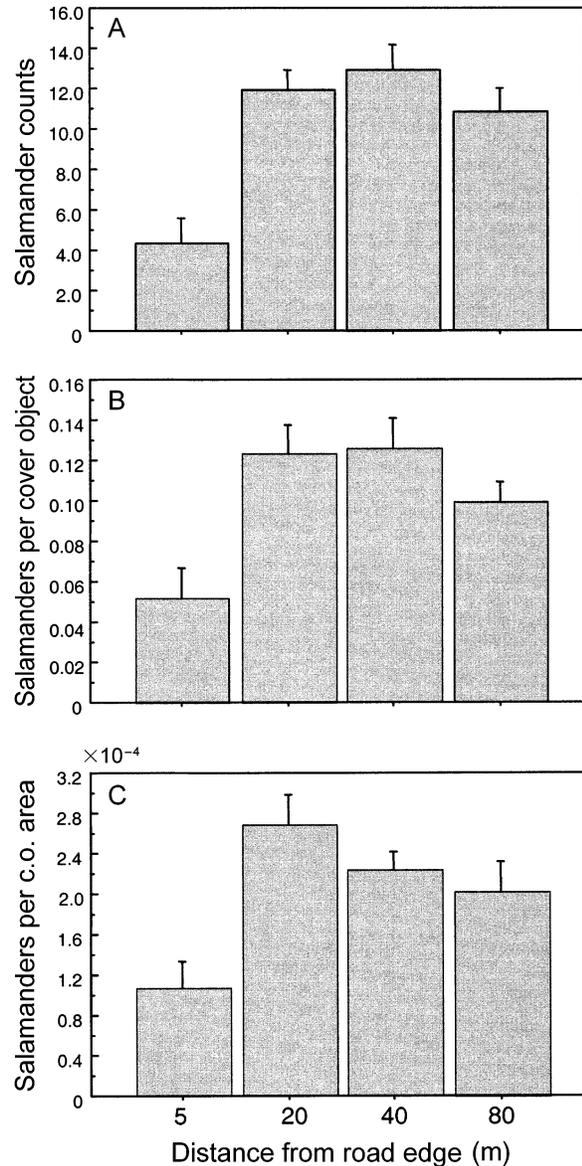


FIG. 1. Red-backed salamander densities at different distances from the road edge for the Mountain Lake 2001 data set: (A) red-backed salamander counts; (B) red-backed salamander counts per cover object; (C) red-backed salamander counts per cm^2 of cover object (c.o.) area. All error bars represent one standard error after removing variation among sites.

of distance ($F_{3,15} = 4.31$, $P = 0.022$), and with significant pairwise differences between the 5-m transects and the 20-, 40-, and 80-m transects. This suggests that the patterns observed in counts did not reflect sampling bias due to changes in the number or size of cover objects. For slimy salamanders, counts were lower and more variable and there was no significant effect of distance from the road edge on counts ($F_{3,15} = 0.62$, $P = 0.61$).

TABLE 1. Analysis of the effects of distance from the road edge on measures of habitat variables.

Variable	Change with distance from road	<i>F</i>	df	<i>P</i>
Mountain Lake, 2001				
Moisture	increase	2.83	3, 20	0.074
Temperature	no change	0.68	3, 20	0.611
Cover object area	increase	4.42	3, 20	0.020
Cover object number	no change	1.13	3, 20	0.369
Big Levels, 2002				
Moisture	no change	0.56	3, 32	0.650
Temperature	no change	0.15	3, 32	0.931
Cover object area	no change	2.10	3, 32	0.127
Cover object number	decrease	3.14	3, 32	0.043
Leaf litter thickness	no change	1.38	3, 32	0.273
Mountain Lake, 2002				
Moisture	increase	5.73	3, 20	0.008
Temperature	no change	0.51	3, 20	0.681
Cover object area	increase	3.38	3, 20	0.046
Cover object number	increase	4.43	3, 20	0.020
Leaf litter thickness	no change	1.12	3, 20	0.371

Notes: Significance of habitat variables was determined by a general linear model taking into account variation among sites. Leaf litter thickness was not measured as part of the Mountain Lake 2001 data set.

With respect to habitat variables, cover object area showed a significant increase with distance from the road edge, while soil temperature significantly decreased with distance (Table 1). Soil moisture was marginally higher at greater distances (Table 1). The total number of cover objects per transect was not affected by distance from the road edge (Table 1).

Big Levels, spring 2002

At the Big Levels sites, a mean of 2.8 red-backed salamanders and 0.2 slimy salamanders were recorded from each transect. Results for Big Levels were similar to the results for the 2001 Mountain Lake surveys. There was an overall effect of distance from the road edge on red-backed salamander counts ($F_{3,24} = 4.72$, $P = 0.010$, Fig. 2A), and on salamanders per cover object ($F_{3,24} = 6.45$, $P = 0.002$, Fig. 2B), though the results were slightly less clear for salamanders per cover object area ($F_{3,24} = 2.98$, $P = 0.052$, Fig. 2C). Counts of slimy salamanders did not change with distance from road ($F_{3,24} = 0.50$, $P = 0.69$).

For habitat variables, only the number of cover objects was affected by distance (Table 1). Five-m transects actually had more cover objects than other transects, possibly due to the presence of cut branches near roads.

Mountain Lake, summer 2002

In 2002, a mean of 9.1 red-backed salamanders and 1.0 slimy salamanders were recorded from each transect. There was a significant effect of distance on counts of red-backed salamanders ($F_{3,15} = 8.05$, $P = 0.0020$, Fig. 3A). In the post hoc analysis, only the 5- and the 80-m transects were significantly different.

However, linear regression of counts on distance was highly significant ($b_1 = 0.02$, $t = 3.79$, $P = 0.001$), suggesting that counts tended to increase with distance from the road edge out to at least 80 m. Patterns were similar for red-backed salamanders per cover object and for red-backed salamanders per cover object area (Fig. 3B, C). For slimy salamanders, there was again no significant effect of distance on counts ($F_{3,15} = 0.06$, $P = 0.97$).

With respect to habitat features, number of cover objects, cover object area, and soil moisture all increased with distance from the road edge (Table 1). Soil temperature and leaf litter thickness did not change with distance from the road edge (Table 1).

Comparisons across species, years, and regions

Red-backed salamanders and slimy salamanders exhibited significantly different responses to distance from road at the Mountain Lake sites ($F_{3,77} = 6.10$, $P = 0.0009$). Although the linear regression results suggested differences among years at the Mountain Lake sites, the interaction between year and distance was not statistically significant ($F_{3,47} = 1.48$, $P = 0.24$). The interaction between region and distance was also non-significant ($F_{3,57} = 1.75$, $P = 0.17$). Across all Mountain Lake sites, there was no effect of distance from road on mean SVL ($F_{3,33} = 0.87$, $P = 0.47$) or the body condition index ($F_{3,33} = 0.95$, $P = 0.43$).

Because soil moisture and cover object area tended to increase with distance from roads at the Mountain Lake sites, we asked whether sites with steeper gradients in these habitat variables also had steeper gradients in red-backed salamander counts. The steepness of the gradient in soil moisture was a significant pre-

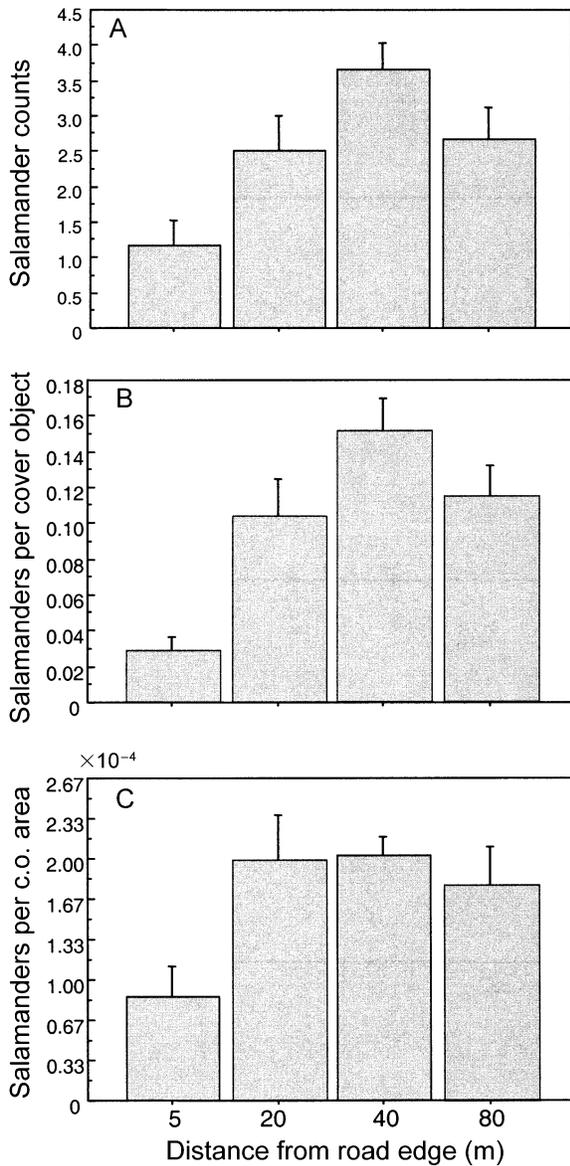


FIG. 2. Red-backed salamander densities at different distances from the road edge for the Big Levels data set: (A) red-backed salamander counts; (B) red-backed salamander counts per cover object; (C) red-backed salamander counts per cm^2 of cover object (c.o.) area. All error bars represent one standard error after removing variation among sites.

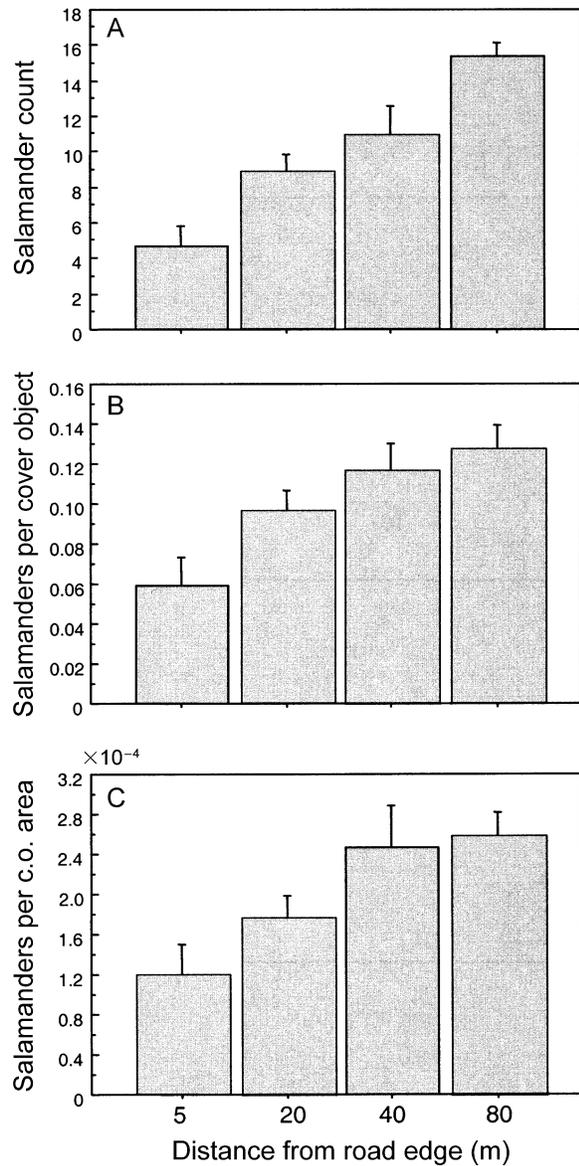


FIG. 3. Red-backed salamander densities at different distances from the road edge for the Mountain Lake 2002 data set: (A) red-backed salamander counts; (B) red-backed salamander counts per cover object; (C) red-backed salamander counts per cm^2 of cover object (c.o.) area. All error bars represent one standard error after removing variation among sites.

dictor of the steepness of the gradient in salamander counts ($R^2 = 0.41$, $b_1 = 36.65$, $P = 0.015$). The steepness of the gradient in cover object area was not a significant predictor of the steepness of the gradient in salamander counts ($R^2 = 0.14$, $b_1 = 0.001$, $P = 0.13$).

Detectability experiment

Red-backed salamanders were detected at approximately equal rates under cover objects during the day in edge vs. interior enclosures (detection probability = 0.391 ± 0.094 vs. 0.371 ± 0.104 [mean ± 1 SE], $F_{1,20}$

= 0.01, $P = 0.93$). Detection rates of salamanders crawling on the leaf litter at night were also indistinguishable between the edge and interior enclosures (detection probability = 0.089 ± 0.024 vs. 0.076 ± 0.018 , $F_{1,21} = 0.80$, $P = 0.80$). We note that the high variation among enclosures gives this experiment limited power, though the observed detectability of salamanders in the edge enclosures was slightly higher than the detectability in the interior enclosures, and thus not consistent

with a bias that could explain differences in our transect counts.

DISCUSSION

Red-backed salamanders showed reductions in counts near road edges in all three data sets. The spatial scale of edge effects was <20 m in two of the three data sets, though salamander counts increased linearly with distance up to at least 80 m at the Mountain Lake sites during the drought of 2002. Slimy salamanders were not reduced near road edges in any of the surveys, although counts of slimy salamanders were low and variable. Taking into account this sampling error, slimy salamanders still showed significantly different responses to roads from red-backed salamanders. Both the area of cover objects and soil moisture increased with distance from road edges, while soil temperature, cover object number, and leaf litter thickness either did not vary with distance from road or did not show consistent patterns of variation. Sites with steeper gradients in soil moisture also had steeper gradients in salamander abundance.

Collectively, these results suggest a role for soil moisture in explaining at least some of the variation in edge effects among years, sites, and species. During the summer drought of 2002 (May–September rainfall = 410 mm), salamander counts continued to increase out to at least 80 m into the forest. During the relatively wetter summer of 2001 (May–September rainfall = 571 mm), there was no evidence that the effects of roads on counts extended beyond 20 m. Variation in the magnitude of road effects across sites was also consistent with a role for soil moisture. Sites with steeper gradients in soil moisture from the road to the interior forest also had steeper gradients in salamander counts. This was not true for cover object area, another variable that tended to increase with distance from road. Finally, differential responses to soil moisture could explain why slimy salamanders were not reduced near roads, while red-backed salamander counts were reduced >50%. Slimy salamanders are larger than red-backed salamanders, have a higher surface area to volume ratio, and have lower dehydration rates than do red-backed salamanders (Grover 2000). However, the size of red-backed salamanders did not vary with distance from road, which might be taken as evidence against the hypothesis that larger bodied amphibians will be less affected by road edges. Additionally, the correlational nature of the data implies that these patterns should not be considered conclusive in themselves. The apparent relationship between moisture gradients and salamander counts could be driven by some other factor that covaries with soil moisture, such as invertebrate abundance (see Haskell 2000) or dust prevalence (Auerbach et al. 1997). Future experiments should help to clarify the role of soil moisture in driving edge effects in salamanders.

The spatial scale of the edge effects that we observed was variable, though comparable to the scale of edge effects observed with other types of edges. For example, deMaynadier and Hunter (1998) quantified the spatial scale of edge effects on amphibian abundance across conifer plantation–mature deciduous forest edges and regenerating clear-cut–forest edges. They found that red-backed salamander abundance within forest was reduced up to 25–35 m from the forest edge. Edge effects were similar for mole salamanders (*Ambystoma maculatum* and *A. laterale*) and for wood frogs (*Rana sylvatica*). Similarly, deGraaf and Yamasaki (2002) found that counts of red-backed salamanders peaked at ~20 m from mature forest–young forest edges. These edge effects are similar to those we observed for the Mountain Lake 2001 and Big Levels data sets, but somewhat smaller than what might be inferred from the Mountain Lake 2002 data set. This comparison suggests that although roads may create only narrow openings in the forest canopy, edge effects from roads can be at least as strong as edge effects from clear-cuts or other types of edges. This is consistent with suggestions that edge contrast, which is very strong at forest–road edges, may be important in determining the magnitude of edge effects (deMaynadier and Hunter 1998).

The similarity of our results for analyses of total salamander counts, salamanders per transect, and salamanders per cover object area suggest that sampling biases did not contribute to our results. The detectability experiment further supports the use of surface transect counts as reliable indices of salamander abundance. These findings are consistent with the results of Smith and Petranka (2000) and Hyde and Simons (2001), who found that surface counts of terrestrial salamanders were highly repeatable and closely correlated with estimates from more labor-intensive techniques. Our study suggests that the utility of surface counts holds across gradients in habitat quality.

One limitation of our study is that it was restricted to the edge effects of roads on salamander counts. Roads may affect animal populations in several other ways. First, roads may reduce dispersal among bisected forest patches. Several studies have suggested that these effects might be important for terrestrial salamanders, including red-backed salamanders (Gibbs 1998a, deMaynadier and Hunter 2000). Second, roads may affect animals' reproduction or survival rates. These effects may not be apparent in count data when animals move between edge and interior habitats.

Another limitation of our study is that we only examined the effects of gravel roads. We chose to examine this road type because these are the most accessible forest roads within our study regions. However, dirt roads, paved road, and occasionally highways may also pass through forest habitats, and the edge effects of these roads may differ from those of gravel roads (Forman and Alexander 1998). Wider roads, certainly, could increase the strength of edge effects. The

effect of road surface is a more complex issue. Paved roads likely absorb more heat than do gravel roads, which could increase the strength of abiotic edge effects on surrounding forest. However, dust from gravel roads could also contribute to changes in the chemical composition and albedo of surrounding habitats (Auerbach et al. 1997). Thus, it is not necessarily obvious how edge effects from other types of roads may differ from those described here.

A final issue is that the species analyzed here may provide a conservative estimate of the edge effects of roads. Red-backed salamanders and slimy salamanders were the most common species in our study area. Thus, one might expect these species to be less sensitive to roads and other habitat disturbances. Indeed, the Southern Appalachians were almost entirely deforested by the turn of the 20th century (Wilcove et al. 1986). The salamander community found today represents the survivors of previous deforestation, and current patterns of abundance may still reflect this land-use history. Red-backed salamanders, in particular, have been shown to be relatively less sensitive to the effects of landscape-scale fragmentation (Gibbs 1998b), and slimy salamanders may be one of the least affected by desiccation (Grover 2000). Additional studies with other species and in regions with less of a history of disturbance could help elucidate these issues.

Given these limitations, our study does have some basic implications for forest management. Primarily, construction of roads does appear to reduce the quality of adjacent forest for at least some terrestrial amphibians, and likely other species that rely on similar habitats. Reductions in salamander counts occurred over a relatively narrow range in two of the three data sets, but appeared to extend at least 80 m in the third data set. This raises the possibility that edge effects from roads could interact with other factors (e.g., drought) to cause nontrivial edge effects for forest-dependent species. We used a geographic information system (GIS) to calculate the amount of forest within 20 and 80 m of roads in the Jefferson National Forest of Virginia and West Virginia. We found that 3.26% of forest area was within 20 m of a forest road, while 11.96% of forest area was within 80 m of a forest road. At least for the 80-m buffer, this analysis demonstrates that a substantial proportion of national forest area may be within the edge-effects zone of forest roads.

The second implication of our study is the suggestion that the severity of edge effects for salamanders may be related to reductions in soil moisture. Different strategies for road building and road maintenance (USDA Forest Service 1998) are likely to have variable implications for soil desiccation. For example, salting roads, removing canopy trees from along roadsides, and removing understory vegetation next to roads may all decrease soil moisture adjacent to roads. Our data suggest that road construction and maintenance strategies that minimize soil desiccation will be less dis-

ruptive to amphibian populations in adjacent forests. Conversely, decommissioning roads, which reduces traffic and maintenance costs (USDA Forest Service 1998), may do little to increase amphibian abundance if abundance depends primarily on abiotic edge effects rather than traffic-related factors. We hope that similar studies on other taxa can help produce a useful synthesis for predicting the effects of road development and maintenance strategies on wildlife populations and for guiding road policy in protected areas.

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